

Figure 3. *Attiliosa bozzettii* Houart, 1993. IRSNB IG27.873/454 (Holotype); height 17.0 mm, maximum diameter 10.1 mm. Locality: Ras Hafun, Somalia, 150–200 m. a. Apertural view. b. Abapertural view. (Photographs courtesy of R. Houart)

2, 5, 7) and at least in one species of *Calotrophon* (Vokes, 1992: pl. 19, fig. 11), but no clearly delineated posterior channels are formed in species of *Panamurex* or *Takia*.

Despite this consistency, we regard our generic placement as tentative due to the low number of potentially informative characters in the type material. This problem is attributable, in part, to poor preservation, since the protoconch and early teleoconch whorls are missing in the holotype. More problematic, however, is the relatively simple morphology of the new species, a condition that characterizes a number of sub-lineages within the *Poirieria* clan and has been a prime source of systematic confusion in the Muricinae (Vokes, 1992, 1999). Strengthening our position somewhat is the close morphological resemblance of *A. aenigma* to the living *Attiliosa bozzettii* Houart, 1993 (Figure 3) from deep waters off the coast of Somalia. Both *A. aenigma* and *A. bozzettii* exhibit paired (or bisected) cords, a rounded rather than a shouldered body whorl, and up to four rather than only three columellar nodules, although these characters vary somewhat in *A. bozzettii* (Roland Houart, 2001, personal communication). These species differ in the more pronounced posterior channel in *A. aenigma*.

Similarities to other species of *Attiliosa*, however, even

to the early fossil taxa, are generic only. *Attiliosa aenigma* differs from the undescribed early Oligocene species from France in having a less angulate and sloped body whorl, a broader parietal shield, heavier spiral ornamentation, and a stronger posterior channel. *Attiliosa aenigma* differs from the next earliest New World species, *Attiliosa gretae* Vokes, 1999, of the late early Miocene of Florida, in having a less angulate body whorl, a broader parietal shield, heavier spiral ornamentation, spiral cords of equal rather than unequal strength, a weaker anal channel, and a less recurved siphonal canal.

The new species superficially resembles *Panamurex rutschi* Vokes, 1992 (Vokes, 1992: pl. 11, figs. 1–4) from the Pliocene Punta Gavilán Formation of Venezuela, particularly in the morphology of the axial ribs, apertural lirae, and columellar nodules; however, *P. rutschi* differs in lacking the prominent anal channel and in having thicker, unpaired, and more widely spaced cords on the body whorl. Older species of *Panamurex*, particularly the Paleogene and early Neogene species, all have open spines on the body whorl and siphonal canal, and thus are very different from *A. aenigma*, which lacks spines altogether.

The paired condition of the spiral cords in *A. aenigma* and *A. bozzettii* is noteworthy because the occurrence of similar spiral ornamentation in a number of species of *Takia* (see above), including one of its geologically oldest species, *Dermomurex (Takia) cookei* MacNeil MS in Vokes, 1975, may indicate a closer phylogenetic relationship between *Attiliosa* and *Takia* than previously recognized. Until now, *Attiliosa* has been compared only to *Panamurex* or *Calotrophon* (Vokes, 1971, 1976, 1992, 1999). Detailed studies of the ontogeny of this character and cladistic methods are necessary to determine whether the paired condition is homologous in these different groups. We draw attention to this condition primarily because it has been ignored in past species descriptions and systematic reviews in the literature.

A second fossil muricid (Figure 4) collected from Terramar 01 could be referable to *A. aenigma* because of its nearly identical shell shape, size, and paired spiral cords. However, the axial ribs of this second specimen are narrower, and the columellar nodules are more prominent than in the holotype of *A. aenigma*. Additional material is needed to determine whether this specimen should be included in *A. aenigma* or whether it represents yet another undescribed species.

The discovery of *A. aenigma* has significance for our understanding of the biogeographic history of the genus. Although Vokes (1989, 1992, 1999) proposed that the genus originated in the Old World during the Paleogene and migrated westward in post-Paleogene times, the latest Eocene/earliest Oligocene age of *A. aenigma* and its occurrence in the New World questions this interpretation. Although age resolution of the European material and sampling resolution of the Paleogene fossil record are too

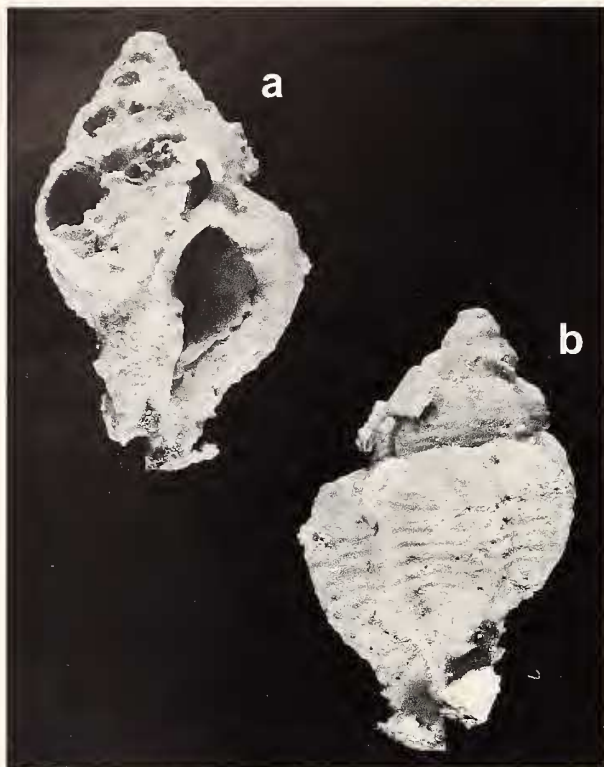


Figure 4. *Attiliosa* sp. cf. *A. aenigma* Herbert & Portell. UF 104450; height 19.0 mm, maximum diameter 11.3 mm. Locality: Terramar 01 (PO017), Suwannee Limestone, Polk County, Florida. a. Apertural view. b. Abapertural view.

poor to determine when and where *Attiliosa* first evolved, the timing and geographic position of the new species indicates, at the very least, that diversification and geographic range expansion in *Attiliosa* were occurring much earlier than previously thought. Future studies should concentrate on refining the systematics of Paleogene Muricidae from the Old World. Are there additional undescribed or "lost" taxa referable to *Attiliosa* and/or closely related groups, and, if so, what do they tell us about character evolution and biogeographic patterns within the Muricinae?

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Latitudinal Gradients in Body Size and Maturation of *Berryteuthis anonychus* (Cephalopoda: Gonatidae) in the Northeast Pacific

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Abstract. Trends in body size and maturation with latitude of the gonatid squid *Berryteuthis anonychus* in the northeast Pacific are described. Squid were collected during May 1999 at seven stations along 145° and 165°W between 39° and 49°N. Mantle lengths ranged from 10.3 to 102.2 mm and increased significantly in both sexes from south to north. Females were both larger and more numerous than males at the northern stations. Both sexes showed a clear pattern of increasing maturity from south to north, and at each station, males were generally in a more advanced stage of maturity than females. Most mature males occurred at the northernmost stations. No mature females were collected. Our data suggest that *B. anonychus* migrates northward in the northeast Pacific during spring, with males maturing at a smaller size than females.

INTRODUCTION

Most studies of squid migration have been conducted on commercially important species that occur relatively near shore. Some of these species, such as *Todarodes pacificus pacificus* (Steenstrup, 1880), *Dosidicus gigas* (d'Orbigny, 1835), and *Illex illecebrosus* (Lesueur, 1821), have been shown to migrate over long distances (> 1500 km) between low-latitude spawning grounds and high-latitude feeding grounds (Hanlon & Messenger, 1996). Few studies, however, have examined the migration patterns of more oceanic species.

Berryteuthis anonychus Percy & Voss, 1963, is a small (mantle length to 150 mm), oceanic squid distributed mainly in the northeast Pacific (Roper et al., 1984). It is a major prey for salmonids (Percy et al., 1988), Pacific pomfret (*Brama japonica* Hilgendorf, 1878; Percy et al., 1993), and neon flying squid (*Onmastrephes bartramii* (Lesueur, 1821); Percy, 1991). Despite its importance in the food web of the subarctic North Pacific, little is known about its life history. In the present study, inferences are made on the migration and spawning of *B. anonychus* in the northeast Pacific based on trends in body size and maturation with latitude.

MATERIALS AND METHODS

Berryteuthis anonychus was collected as by-catch during a United States National Marine Fisheries Service survey of salmon in the northeast Pacific (Carlson et al., 1999). Samples were collected during 6 to 17 May 1999 at seven

stations along 145° and 165°W between 39°01' and 49°03'N (Figure 1). Sampling was conducted from just before dawn to just after dusk. Both longitudinal transects were sampled in different directions (145°W—south to north; 165°W—north to south), and there was no diel pattern to the times at which stations were occupied, thus eliminating the possibility that any trends in body size and maturation with latitude seen in the data might have been due to sampling bias. At each station, a midwater trawl modified to fish at the surface was towed for 1 hour. The trawl was 198 m long with hexagonal mesh in wings and body, and a 1.2 cm mesh liner was used in the codend. Trawling speeds were 7–9 km hr⁻¹, and the average net dimensions while fishing were 16 m vertical spread and 45 m horizontal spread. Subsamples of the total catches were taken at the two stations (#11 and #31) where more than 400 squids were collected. A total of 359 *B. anonychus* specimens, including 195 males and 164 females, were examined in the following analyses. Specimens were sexed, and the dorsal mantle length of each was measured. A modified version of the maturity scales described by Lipinski & Underhill (1995) was used for maturity analysis (Table 1). The buccal membrane and inner mantle wall of each female were examined for the presence of discharged spermatophores or spermatangia (sperm vesicles) to determine if any had mated before collection.

The relationship between latitude and mantle length was evaluated using standard regression analysis, and the significance of the population regression was tested using analysis of variance (Zar, 1996:338–343). Normality of the size-frequency distribution at each station was tested using normal quantile plots (Sokal & Rohlf, 1995:118–122). Male and female mantle sizes were compared at

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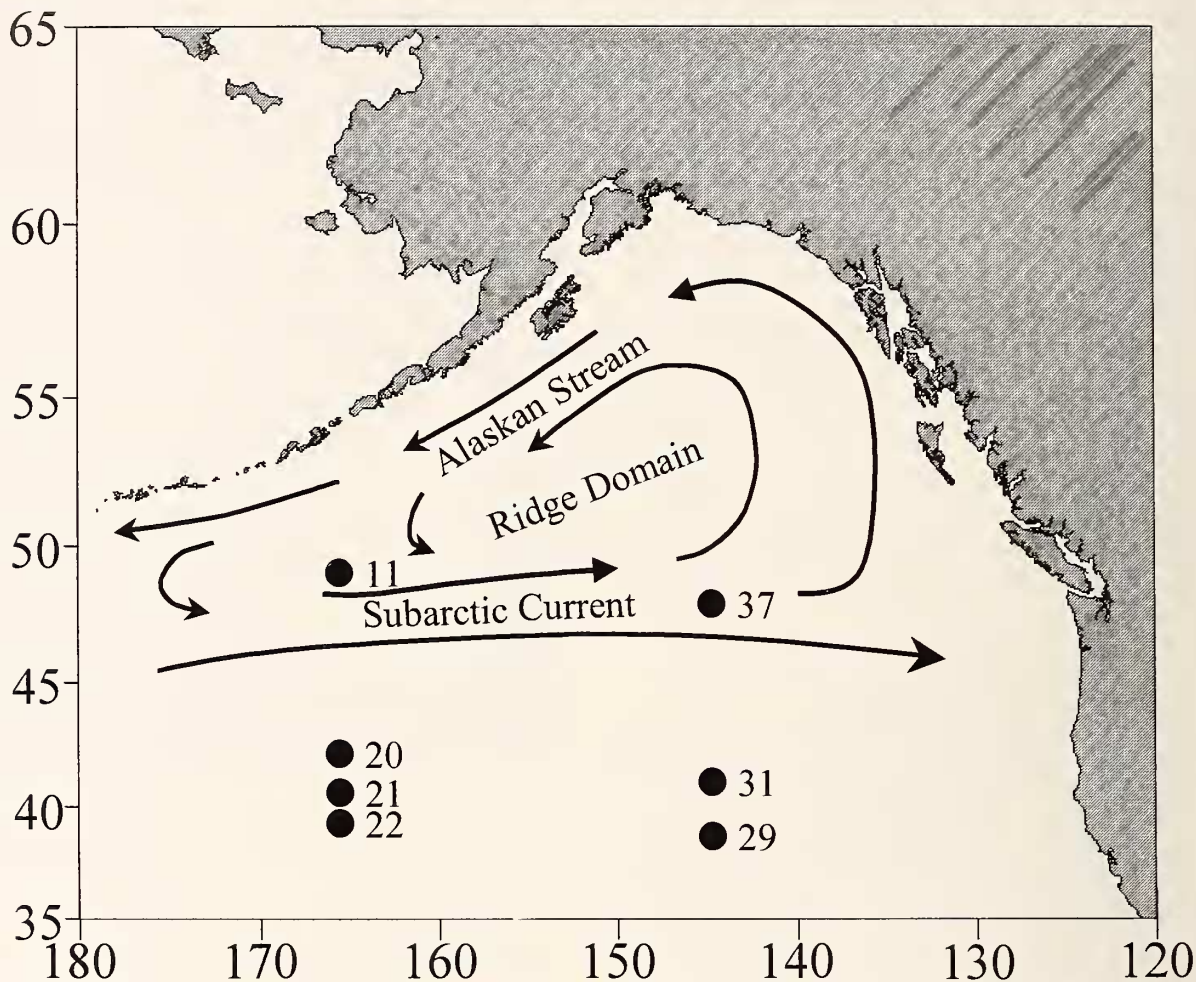


Figure 1. Map of the Northeast Pacific showing sampling stations where *Berryteuthis anonychus* was collected and the long-term mean circulation (adapted from Musgrave et al., 1992). Station numbers correspond to those of Carlson et al. (1999).

each station using the Mann-Whitney test. The relationship between latitude and the proportion of females in the catch was evaluated using Chi-square analysis (Zar, 1996: 562–565); the two southernmost stations, where more than 20% of the samples could not be sexed, were excluded from this analysis. The relationship between maturity stage (dependent variable) and latitude (independent variable) was examined using polytomous logistic regression. Significance in all tests was accepted at the $P = 0.05$ level.

RESULTS

Size

Mantle lengths (ML) ranged from 10.3 to 102.2 mm and increased significantly in both sexes from south to north (Figure 2, Table 2). Station #22 was exceptional in having a wide size range (10.3–75.7 mm ML), including eight specimens larger than 64 mm ML. Size-frequency

data are normally distributed at all other stations except #11, where data are negatively skewed due to differences in size and abundance of males and females.

Sex

Females were both larger and more numerous than males at the northern stations. At each station north of 42°00'N, male and female sizes differed significantly. This size difference was most distinct at Station 11, where the mean female size was 14 mm larger than that of males. The proportion of females in the catches increased from south to north (Table 2) and followed a significant linear trend. No females had discharged spermatophores or spermatangia present in the buccal membrane or inner mantle wall, suggesting that none had mated before collection.

Table 1

Maturity scale used for *Berryteuthis atonychus* (adapted from Lipinski & Underhill 1995). ML, mantle length; NG, nidamental gland; NGL, nidamental gland index = NG length/MLX100; NS, Needhams' sac; OG, oviducal gland; OM, oviducal meander; PL, penis length (distance from the anteriormost part of the spermatophoric complex to the distal (anterior) end of the penis); PLI, penis length index = PL/MLX100; S, spermatophores; SC, spermatophoric complex.

Stage	Male stage description					Female stage description					
	Testis	Separate parts of SC visible	PLI	S in NS	S in penis	Mantle thin and/or flaccid	Ovary	Nidamental glands	Oviducts	Ovaries contain mature oocytes	Mantle thin and/or flaccid
I Juvenile	transparent	no	< 5	0	0	no	translucent	small and transparent; NGI < 6	not visible	no	no
II Immature	whitish; structure not visible	yes	< 5	0	0	no	opaque	transparent or opaque; NGI < 6	not visible	no	no
III Preparatory	whitish; structure not visible	yes	5-15	0	0	no	opaque	enlarged and opaque; NGI > 6	visible; contain no eggs	no	no
IV Maturing	whitish; structure visible	yes	>15	≤2	0	no	opaque	opaque; NGI > 6	visible; OM contain a few eggs	a few	no
V Mature	whitish; structure visible	yes	>15	densely packed	present	no	opaque	opaque; NGI > 6	visible; OM contain many eggs	many	no
VI Spent	whitish; structure visible	yes	>15	few	present	yes	opaque	opaque; NG > 6	visible; few eggs remain	yes	yes

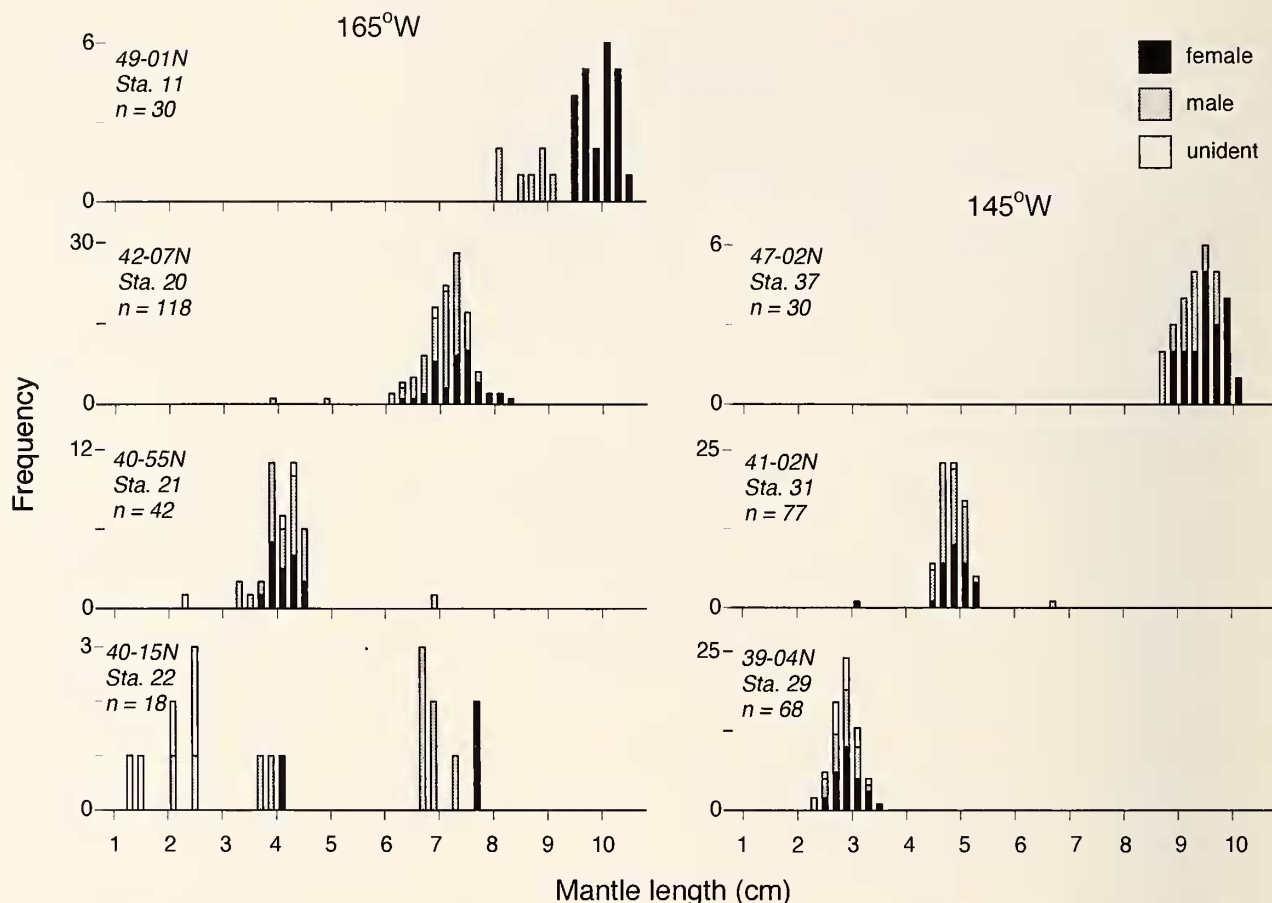


Figure 2. Frequency distributions for mantle size of *Berryteuthis anonychus* collected in the northeast Pacific along 145° and 165°W.

Maturity

Both sexes showed a clear pattern of increasing maturity from south to north (Figure 3), and the relationship between maturity stage and latitude was significant. At each station, males were generally in a more advanced maturity stage than females. Mature (stage V) males occurred at four stations between 40°15' and 49°01'N and

ranged in size from 64.1 to 94.8 mm ML; 71% were collected at the two northernmost stations. The seven mature males collected at and south of 41°02'N differed significantly in size from those at the two northernmost stations (Mann-Whitney test, $P < 0.001$). Of males larger than 75.8 mm ML, 94% were mature. Females ranged in size from 23.3 to 102.2 mm ML, but none were mature. Of the most advanced female maturity stage collected (stage III), 89% were collected at the two northernmost stations. The five stage III females collected at and south of 42°07'N differed significantly in size from those at the two northernmost stations (Mann-Whitney test, $P < 0.001$). Station #22 was again exceptional in being the only southern station where advanced maturity stages of both sexes were collected.

Table 2

Median mantle length (ML) and % of females in the catch of *Berryteuthis anonychus* at each station.

Latitude (N)	Longitude (W)	Station #	Median ML (mm)	Female %
49°01'	165°	11	95.7	77
47°02'	145°	37	92.2	63
42°07'	165°	20	69.6	38
41°02'	145°	31	46.5	42
40°55'	165°	21	39.3	39
40°15'	165°	22	38.1	
39°04'	145°	29	26.8	

DISCUSSION

Berryteuthis anonychus collected during spring in the northeast Pacific increased in size and maturity from south to north. Didenko (1990, in an abstract from the 5th All-USSR Conference on Commercial Invertebrates in 1990) reported similar trends in size and maturity with

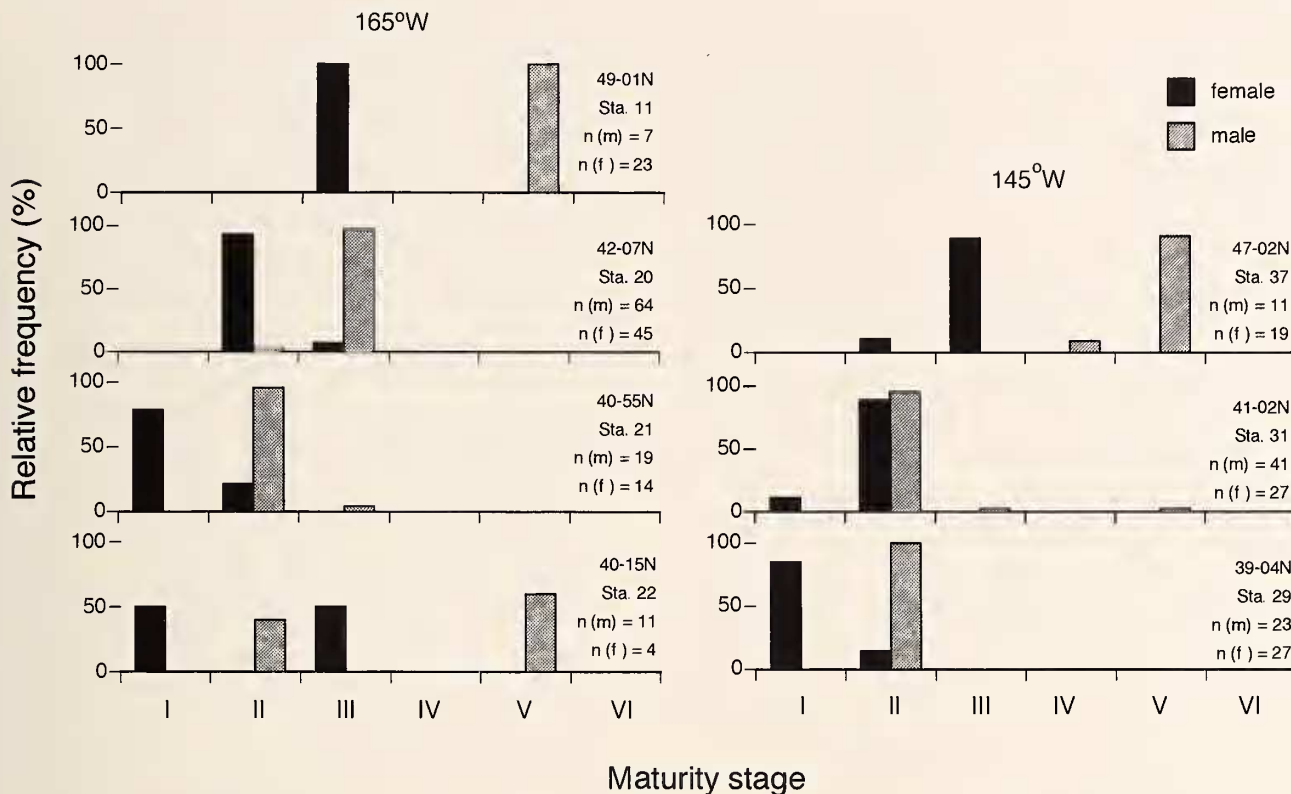


Figure 3. Relative frequency distributions for maturity stage of *Berryteuthis anonychus* collected in the northeast Pacific along 145° and 165°W.

latitude in this area during spring and summer. In the absence of known northward currents in this area, the simplest explanation for these patterns is that *B. anonychus* actively migrates northward during spring and summer.

Ommastrephes bartramii, another pelagic squid distributed widely in the North Pacific (Clarke, 1966), shows a similar trend of increasing size with latitude as it migrates northward during summer and fall. It hatches in subtropical waters, migrates to feeding grounds north of 41°N, then returns south of 32°N to spawn (Murata & Nakamura, 1998). As it migrates northward along 165°W, modal mantle lengths increase from 15 cm near 37°N to 40 cm near 46°N (Murata & Hayase, 1993), which is a mean increase in mantle length of about 19% per degree latitude. *Berryteuthis anonychus* modal mantle lengths in the present study increased from about 3 cm near 39°N to about 10 cm near 49°N, for a similar mean increase in mantle length of about 23% per degree latitude.

The sizes of *Berryteuthis anonychus* found in predator stomachs collected in the Subarctic Current in the northeast Pacific during summer roughly correspond with the relation between body size and latitude seen in the present data. Pacific pomfret (*Brama japonica*) at 49–52°N prey heavily on > 70–80 mm ML squid (Pearcy et al., 1993),

and salmonids at 45°30'–51°N prey heavily on 80–100 mm ML squid (Pearcy et al., 1988). In the Ridge Domain and Alaska Stream north of the Subarctic Current, small (< 60 mm ML) *Gonatopsis* spp. squids replace the larger *B. anonychus* as the main cephalopod prey of both Pacific pomfret and salmonids (Pearcy et al., 1988; Pearcy et al., 1993), suggesting that it becomes more difficult to prey on *B. anonychus* as it increases in size.

Males matured at a smaller size than females. These data are consistent with those of other gonatids, including *Berryteuthis magister magister* (Berry, 1913), *Gonatopsis borealis* Sasaki, 1923, and *Gonatopsis onyx* Young, 1972 (Arkhipkin et al., 1996; Nesis, 1997). The occurrence of small maturing specimens south of 41°N suggests that early maturing forms may occur in southern waters. Early- and late-maturing groups have been reported in other pelagic squids, including *G. borealis*, and the ommastrephids *Sthenoteuthis pteropus* (Steenstrup, 1855), *S. onal-anienensis* (Lesson, 1830), and *Dosidicus gigas* (Nesis, 1997; Masuda et al., 1998).

Both sexes were of similar size and abundance at southern stations, but females became larger and more numerous than males at the northern stations. Differential growth of the sexes is common in cephalopods as they approach maturity (Forsythe & Van Heukelem, 1987),